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HEAT PRODUCTION OF HONEYBEES IN WINTER.

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CONTENTS.

Studies of the behavior of honeybees in winter [1] show that these insects do not hibernate, but throughout the entire winter they consume their stores of honey and generate heat. The results of these studies further show that after the winter cluster is formed, at 14° C., there is an inverse relationship between the temperature inside and outside the cluster, and that the generation of heat to warm the winter cluster is solely by muscular activity, such as fanning of the wings and other movements. These results do not agree with the conclusions of Parhon [2] that the honeybee is in part heterothermic. The work on behavior of the bees during winter, from which the practical conclusions as to the needs of bees in winter were drawn, was chiefly on temperature responses, and no data were available as to the actual heat production of the bees during this season. The work herein recorded was begun in order that the missing data might be in part obtained.

From many observations it has long been known that the duration of life of the individual worker bees is determined by the work which

[1] U. S. Dept. Agr. Bul. 93 (1914), The Temperature of the Honeybee Cluster in Winter. By Phillips and Demuth. See also Farmers' Buls. 695, 1012, and 1014.

[2] Parhon, Marie, 1909. Les échanges nutritifs chez les abeilles pendant les quatre saisons. Paris: Masson et Cie. 57 pp.

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they are called upon to do. When there is a heavy honey flow and the bees are at their greatest activity their lives are limited to about 6 weeks, while during the winter season, if every condition is favorable, they may live 6 months. On the other hand, it is clear from the experience of beekeepers and from the investigations previously mentioned that if the conditions in wintering are unfavorable the bees are aroused to great activity. Under these conditions they are greatly reduced in strength, and even though they may live through the actual period of winter, they are so depleted in vitality that they are unable to do the heavy work incident to building up the colony to full summer strength, and they die off faster than their places are taken by the emerging bees of the brood reared in the spring. In the honeybee organism either the power of constructive metabolism is entirely lacking or it is far less effective than that of destructive metabolism, and the rate of the latter is apparently accelerated by the activity of the bees, thus bringing on more rapidly the impairment of functional capacity which ends in death. The physiological changes which occur in worker bees during this process of aging are not well understood, but certain facts have been observed which are significant. Mr. Goodrich-Pixell[3] has found that the nerve cells in bees dying of exhaustion are highly vacuolated and the cytoplasm greatly depleted, thus substantiating the work of Hodge[4] and of Smallwood and Phillips.[5]

Chief among the factors that influence the activity and consequent welfare of a colony of bees in winter are the condition of the colony at the beginning of winter (physiological age of the individuals), external temperature, quality of the food used during confinement, ventilation, humidity, and various causes of irritation. The experiment here recorded was undertaken to study the responses of bees to some of these stimuli, as measured by heat production, being a continuation of the work of Phillips and Demuth (loc. cit.) on the behavior of bees in winter, in which work the temperature responses were of greater significance. It was carried out in December, 1915, and the intention was to continue with similar experiments in other seasons under a wider variety of conditions than was maintained in this instance. Such investigations can be conducted only after brood rearing has normally stopped, and they must be concluded before the bees are filled with feces, in order that the data may not be complicated by activity due to this disturbing factor. It is therefore

[3] Quart. Jour. Micros. Sci. [London], n. ser., 64 (1920), No. 254, Pt. 2, pp. 191–206. ill. Determination of age in honeybees.

[4] Jour. Physiol, 17 (1894) Changes in ganglion cells from birth to senile death; observations on man and honeybees.

[5] Jour. Comp. Neur., 27 (1916). Nuclear size in the nerve-cells of the bee during the life-cycle.

possible to carry out but one experiment a year with a given colony. Circumstances incident to the war prevented continuation of this work, but the results obtained in this experiment are of such economic importance, as well as scientific interest, that it seems desirable to publish them without further delay.

SOURCE OF HEAT IN THE WINTER CLUSTER.

The effect of external temperature on the activity of a colony of bees is conspicuous. The bee is similar to other cold-blooded animals in that it lacks the means for internal regulation of body temperature that are found in birds and mammals, and hence the temperature of its body is affected by that of the surrounding air. As the temperature of the air in the hive falls in winter the bees become less active until a certain critical temperature (14° C.) is reached, at which they undertake by muscular activity, not unlike that of shivering, to produce heat in order to keep warm. Between the combs and sometimes extending above or below them they form an approximately spherical and fairly compact cluster, with the bees on the outside comprising a sort of shell with their heads turned toward the center. This shell may be several layers thick, the number of layers and the compactness of the cluster depending upon the size and condition of the colony and the temperature of the air in the hive. The bees in this shell remain quiet, except for an occasional shifting of position, but those in the space inside the shell become very active, moving about, shaking their bodies, and fanning vigorously with their wings, thus producing heat to warm the cluster.

By means of many thermocouples fastened in different parts of the hive Phillips and Demuth (loc. cit.) were able to measure the temperatures at various points within and around the winter cluster. They found that when the temperature of the air within the hive and surrounding the bees was between 14° and 20° C. the bees remain quietly on the combs but not clustered, their body temperatures being, of course, approximately that of the surrounding air. While the upper temperature limit of this quiescent condition is not definitely fixed, varying with the condition of the bees and the weather outside the hive, the lower limit is quite accurately determined by the needs of the bees. When the air temperature falls to 14° C. the bees come together to form the winter cluster. If the temperature falls still lower, they begin to generate heat within the cluster, and frequently the inner temperature rises considerably above those temperatures at which the bees were able to exist without activity. Temperatures as high as 30° to 35° C. are not uncommon, and, indeed, were observed even when the air outside the cluster was as low as

0° C. In locations where the outer temperatures fall much below this the bees are still able to maintain high temperatures, more bees taking part in heat production. That such high temperatures can be maintained in these circumstances indicates that the shell of bees is effective as a heat insulator, but there is obviously a serious drain on the vital capacity of the bees employed in producing heat. This is shown by the rapid slowing down of the fanning of the wings as it continues.

OUTLINE OF THE EXPERIMENT.

To obtain information regarding the actual amount of work done by a colony of bees while in the winter cluster, a small colony on four combs having natural honey stores was placed in the chamber of a small respiration calorimeter and their carbon-dioxid production and oxygen consumption were measured for 10 days, while the temperature of the air surrounding the bees was kept just low enough so that the bees at all times would remain clustered. Throughout the experiment the temperature of the air surrounding the bees and at several points within the cluster was taken in order that this work might be made comparable with the work on the behavior of bees in winter as indicated by temperature responses. The bees were located in a box within the calorimeter so constructed that while they could not escape from it there was opportunity for abundant ventilation. There were 14 thermocouples distributed in the hive in the calorimeter in such manner that the temperatures in different places inside and outside the cluster could be ascertained, the leads from the thermocouples being extended through the outlet in the wall of the chamber to a potentiometer on the outside. The temperatures were read every half hour, day and night, for nearly 12 days.

The thermocouples were so placed in the hive as to make it impossible for the clustered bees ever to occupy space in which some of the thermocouples were not located, thus insuring that the temperatures of the cluster might be obtained wherever the cluster might move in the hive. The temperatures of all parts of the hive outside the cluster could also be obtained by the arrangement of these thermocouples. One of the thermocouples (No. 15) was located outside the hive and 2 inches from it, thus giving the temperature of the air of the chamber at this point. The readings obtained with this thermometer are plotted in the charts on pages 15 to 18. A resistance thermometer was also placed in the chamber, but at some distance from the thermocouple. Measurements made with this thermometer are shown in the table on page 8. The two records did not always exactly agree because the thermometers were not together.

DISCUSSION OF THE TEMPERATURE RESPONSES IN THIS EXPERIMENT.

The colony used in the experiment here reported was taken to Washington from the suburbs some time prior to the beginning of the experiment. The bees were placed in the calorimeter and then it was found that the apparatus was defective and it was necessary to remove them. During the interval before the experiment here recorded was begun, they were placed outside where they were free to fly when the weather permitted, and they had several flights and carried out the dead bees. They were therefore in good condition at the beginning of the experiment.

For several hours after the hive was again placed in the respiration chamber, the temperatures of the hive and bees were high, chiefly as a result of the disturbance arising from the handling necessary at this time. They were put in place at 3 p. m. on December 11, and during the night the temperature of the bees on one occasion, and in one point only, rose to 35° C. During the night the temperature of both the chamber and the bees drifted down, until shortly after noon on the 12th, when they may be considered as having reached normal quiescence. Just when the bees definitely formed a winter cluster is not clear from the data, but certainly when they had reached quiescence they were clustered.

In the graphic charts of temperatures of this colony, records are included for thermocouples 6, 7, and 12, these being the ones which were in the center of the cluster, which was located near the top and slightly to one side of the hive. For comparison with these the record for thermocouple 15 giving the temperature of the air of the chamber at one point outside the hive is also included.

It will be observed that on several occasions the temperature of the center of the cluster (which shifted between thermocouples 12 and 7, according to the movement of the cluster during the experiment) rose somewhat abruptly but temporarily, not, however, reaching the temperatures observed at the time that the bees were placed in the chamber. While some of the rises may be attributed to mechanical disturbances, it was not always possible to determine the exciting cause. This is in accordance with numerous observations made in the work on the behavior of bees in confinement to which reference has already been made. Throughout the experiment, of course, heat production never ceased, and with the bees in this condition of activity it took but a small disturbance to induce them to generate slightly more heat. This is comparable with the periods of activity that have long been observed in bees wintered in cellars.

It is more important to note that during the 12 days that the bees were in the respiration chamber the temperature of the cen-

ter of the cluster gradually rose from an average of 16° C. on December 13 to an average of 30° C. on the 22d, though the air outside the hive kept in the range of temperature from 6° C. to 9° C. This is in agreement with results obtained by Phillips and Demuth (loc. cit.) with bees wintered in a cellar which were interpreted as indicating that such an upward drift of temperature of the colony during confinement is the result of irritation because of an accumulation of feces. In the case of the colonies recorded in an earlier publication,[6] one colony showed a slower rise than was found in this colony, while another, wintered on honeydew stores, showed a more rapid rise. Since it has been shown that disturbance of any sort causes a rise in cluster temperatures, it is not entirely clear to which disturbance the rise of this colony should be attributed. Of course, as this colony was located in a respiration chamber in a busy laboratory, it was exposed to greater disturbance than would have been the case in some other experiments or in the average bee cellar, although all practicable precautions were taken to avoid jar and the apparatus was cushioned. It is not improbable that the sudden and temporary increases in temperature may have been due to physical disturbance and that the cause of the continued rise was physiological disturbance.

It will be noted that beginning at 6.30 p. m. on December 22 the temperatures of the cluster began to drop. At this time the carbon-dioxid content of the air in the chamber was high and the oxygen deficient, as will be explained later. Under these conditions the bees were more quiet (generated less heat) than when under conditions which would usually be considered more favorable. The temperature of the center of the cluster dropped until it reached 23° C. The reason for the decrease in activity at this time has not been discovered. It was thought that the bees were dying because of unfavorable atmospheric conditions, but at 5 a. m. on the 23d the temperature again began to rise and continued until it again reached 34° C. Whether this increase in activity was a reaction in response to physical disturbance or to change in atmospheric conditions made at this time (see p. 13) is not clear.

METHOD OF MEASURING THE WORK DONE BY THE CLUSTER.

At noon, December 12, measurement of the metabolic activity of the bees was begun. The respiration calorimeter used for this experiment has been described in a publication of the department,[7] but to aid in explaining the conditions of the experiment the principles of

[6] U. S. Dept. Agr. Bul. 93. The Temperature of the Honeybee Cluster in Winter.
[7] Jour. Agr. Research [U. S.], 6 (1916), No. 18, pp. 703–720.

the apparatus may be briefly summarized. The respiration chamber in which the hive was inclosed was ventilated by withdrawing air from the lower portion, passing it through sulphuric acid to remove water vapor and through soda lime to remove carbon dioxid, and returning it to the upper part of the chamber. The increase in the weights of the sulphuric acid and the soda lime during a given period indicates respectively the quantities of water vapor and carbon dioxid removed from the chamber. These represent the quantities produced during the period when due allowance is made for change in the water vapor and carbon-dioxid content of the air as ascertained from analyses made at the beginning and end of the period. Oxygen to replace that removed by the bees was supplied to the chamber from a cylinder, the gas being introduced at a rate sufficient to maintain a certain volume in the system, as indicated by a tension equalizing device which served to keep the air in the chamber at the same barometric pressure as that of the laboratory. The quantity of gas admitted was ascertained from the loss in weight of the cylinder or by reading a meter through which the gas was passed. This showed the quantity of oxygen consumed by the bees when correction was made for change in the residual oxygen content of the air of the chamber. In making these corrections for variations in residual gases, changes in temperature and barometric pressure of the air of the system were also taken into account. By proper attention to these means of ventilation, any desired conditions with respect to water vapor, carbon dioxid, or oxygen content of the air could be maintained.

The temperature of the air surrounding the hive could also be controlled to a certain extent. In a space adjacent to the metal walls of the respiration chamber, and protected by a thick heat-insulating cover, were means for heating and cooling the walls; also within the chamber was a coil of copper tubing through which cold water could be circulated to take heat from the air about the hive. By weighing the water flowing through this coil and measuring its increase in temperature, the quantity of heat carried out could be ascertained, which, with necessary corrections for heat from other sources, would be that imparted to the air by the bees.

RESULTS OBTAINED IN THE EXPERIMENT.

Data indicating the physiological activity of the bees are summarized in the following table with others showing the experimental conditions.

Summary of experimental data.

Date.	Temperature of air in the chamber.	Humidity of air in chamber.	CO_2 in air in chamber.	Oxygen in air in chamber.	Water vapor taken from the air.	Carbon dioxid produced.	Oxygen consumed.	Heat generated.
	° *C.*	*Per cent.*	*Per cent.*	*Per cent.*	*Grams.*	*Liters.*	*Liters.*	*Calories.*
Dec. 13	7.3 to 8.8	....	0.53	15.2	17.1	9.6		
Dec. 14	6.4 to 8.0	75 to 90	1.42	16.8	3.4	10.4		
Dec. 15	6.1 to 8.2	77 to 90	.87	17.1	5.0	11.7		
Dec. 16	6.3 to 7.0	77 to 95	.81	21.1	8.1	13.3		
Dec. 17	6.3 to 7.6	72 to 93	1.08	22.6	8.3	12.8		
Dec. 18	7.8 to 9.2	76 to 95	.52	24.5	6.9	12.1		
Dec. 19	7.1 to 7.8	50 to 86	.63	26.4	26.5	12.9		
Dec. 20	6.9 to 7.9	49 to 66	.23	28.9	25.9	14.5		
Dec. 21	6.8 to 8.3	47 to 66	1.40	24.5	22.2	11.0		
Dec. 22	7.4 to 7.7	45 to 65	.51	18.2	23.2	16.3		
Dec. 23	7.6 to 8.8	50 to 55	.29	7.3	15.9	14.9		
Total, omitting first day						129.9	138.4	683

With the warm conditions prevailing in the laboratory, the cooling capacity of the apparatus, which had been constructed for work at higher temperatures, was not sufficient to chill the hive as much as had been desired when this experiment was planned, consequently the bees were not subjected to very low temperatures. Those shown in the table were measured with an electrical resistance thermometer suspended in the air above the hive, which was as warm as that in any part of the apparatus, but the readings on two thermometers in other parts of the chamber did not differ materially from these. The figures shown are the lowest and highest temperatures observed each day, but there was no uniformity in the time at which these occurred. The fluctuations in temperature are shown in the curve for thermocouple No. 15 on pages 15 to 18. The maximum range, from 6.1° to 9.2° C., was in the vicinity of the temperature which beekeepers usually consider favorable for bees wintering in cellars.

The daily production of carbon dioxid shown in the table is an index of the amount of work performed by the bees. This quantity was derived, in the manner previously explained, from the weight of the carbon-dioxid absorber, which was taken every 24 hours. Any error in these figures, with the possible exception of those for December 21 and 22, which are explained later, is believed to be of small magnitude. The most significant error that could occur would be due to the fact that the circulation of air was not directly through the hive, but through the chamber in which the hive was inclosed. In some cases there might be an accumulation of carbon dioxid in the hive in one period which would escape in a later period, with a

corresponding error in the measurements of the quantities for the two periods; but as there was free space in the small experimental hive for only a few liters of air, a relatively large change in the carbon-dioxid content of the air in the hive would introduce only a very small error in the quantity measured in any period.

The determination of the carbon-dioxid production for the experiment as a whole is accurate. In footing the total the quantity for the first day is omitted, because the oxygen consumed was not measured that day. In the 10 days the bees produced 130 liters of carbon dioxid and consumed 138 liters of oxygen. The corresponding respiratory quotient is 0.94, which indicates that their metabolism was almost entirely that of carbohydrate. Their heat production, calculated from these data, was 688 calories. The quantity of heat measured by the calorimeter was larger than this, but it involved an error due to leakage of heat through the walls, owing to the wide difference between the temperature of the air in the chamber and that in the laboratory, which the apparatus as used could not overcome. Making such allowance for this error as was indicated by subsequent test of the apparatus under somewhat similar conditions, the corrected amount of heat measured was but slightly different from this computed value.

The number of bees in this colony, by actual count, was 9,635. The average weight of empty worker bees is about 0.075 gram; their total weight, in round numbers, would be 720 grams. The heat output of this colony, 688 calories, was therefore equivalent to 0.97 calorie per gram for the 10 days, or virtually 0.1 calorie per gram per day. This is equivalent to a heat output of 7,000 calories per day by a man weighing 70 kilograms (154 pounds), which is found only in unusual circumstances. The average individual of this size actively engaged in hard work at least 8 hours a day would give off about 4,000 calories in 24 hours. The heat output of lumbermen working hard in the northern woods in a cold winter was found to be about 7,000 calories per man per day, as indicated by their food consumption. During the period that they were working hardest their hourly expenditure of energy may have been double the average for the rest of the day, possibly as high as 600 calories per hour, although this seems doubtful. In certain experimental conditions a well-trained man engaged in muscular activity sufficient to cause a heat output of 650 calories per hour, which was measured in the same manner as the heat output of the bees was measured in this experiment, but this was considered to be severe, exhausting work, almost at the limit of human endurance, and was continued only for short periods. This output, per unit of weight, would be larger than that of the colony of bees taken as a whole, but it will be recalled that the bees actually

engaged in the excessive activity of heat production at any one time are only a small part of the total colony, the rest of them being crowded together in the shell of the cluster or in empty cells of the honey comb or standing quietly. The amount of work done by the bees that are really active is comparable with that done by the man in unusual conditions, and is therefore relatively enormous; and this is maintained not only for short periods but through the whole day and the whole winter.

Moreover, it will also be observed that the temperature conditions during this experiment were those in which bees are the least active. In fact, as mentioned previously, the temperature in the respiration chamber during the experiment was about the same as that which beekeepers usually maintain in cellars for wintering bees. Colonies wintered outdoors, especially if unprotected, must endure in many cases much more severe temperature conditions. Furthermore, this experiment was conducted at a time of the year when bees are naturally more nearly quiescent. Bees are usually more active during the latter part of winter than during late fall and early winter. The figures obtained in this experiment, therefore, represent about as low an expenditure of energy as is ever found in a colony of bees, except for short intervals. In a preliminary test with this colony the quantities of carbon dioxid measured were decidedly larger than these, owing to less favorable conditions.

A hygrometer suspended in the chamber was read at frequent intervals. The maximum and minimum readings for each day are shown in the table. During the first five days the humidity was allowed to remain at a high level. This was accomplished by keeping the air of the system in circulation only part of the time, virtually every other hour. During the other five days the humidity was kept much lower by maintaining a constant circulation of air through the sulphuric acid. There was a very noticeable difference in the quantities of water vapor removed from the chamber in the several days of the two periods, owing to the fact that the relative dryness of the air in the later period was causing a loss of water from the wood of the hive. No difference in the activity of the bees that could be ascribed to the difference in water-vapor content of the air was noticeable in the temperature curves or in the carbon-dioxid output of the various days.

The barometer was read at noon each day. There were no significant changes in barometric pressure during the course of the experiment. The reading on the 13th was 755 millimeters, which rose each succeeding day to 769 on the 16th, then fell to 750 on the 18th. It was 767 on the 19th and for the rest of the experiment remained within 4 millimeters of this pressure.

There was no apparent effect on the activity of the bees from variations in the carbon-dioxid content of the air in the hive, at least within very wide limits. One column in the table shows the percentage of carbon dioxid in the air at the time the residual analysis was made each day. These figures tell little of the condition of the air at any other period during the day; they merely show what it was after the air of the chamber had been passing through the soda lime for at least an hour; but unless the bees had been actually more active at the time the residual analysis was made (which, according to the thermocouples, did not occur in any instance) there must have been at least as much and probably more carbon dioxid in the air previous to the time of the analysis than is indicated by these figures. It would appear, then, that throughout the whole of the experiment the carbon-dioxid content of the air in the hive was appreciably greater than that of normal air, which is probably the usual condition in a hive; also there were outside variations in the proportion of this gas in the air, as shown by the data in the table. On December 21 and 22 arrangements were made to insure a considerable excess of carbon dioxid in the air. During most of the time on these days the soda lime was removed from the train for purifying the circulating air and the carbon dioxid was allowed to accumulate within the respiration chamber while the water vapor was removed. Starting with the content of nearly one-quarter of 1 per cent on the 20th, or almost eight times that in normal air, the increase continued until in the whole air system of the apparatus, which was about 170 liters, there was included over 10 liters of carbon dioxid before the period ended on December 21, a proportion more than 200 times that in normal air. There is no significant change in the curves on page 18 showing the behavior of the bees, to indicate that they were materially affected by these abnormal conditions. The curve for thermocouple No. 7 continued at the same level for nearly 12 hours, then began to rise slowly; those for Nos. 12 and 6 fell somewhat for about 12 hours and then maintained a level for the remainder of the period. There would appear to be on the whole a quieting of the bees for this day, but this could be hardly attributed to the quantity of CO_2 present, for on the following day, when there was a still greater concentration, the activity of the bees increased.

From the character of the curves in these two days it would be expected that the carbon-dioxid production on the 22d would exceed that of the 21st, but not necessarily by nearly 50 per cent as shown in the values in the table. It is not unlikely that some of the carbon dioxid measured on the 22d was produced on the 21st. Unintentionally, replacement of the soda lime in the air circulating system was delayed until one hour before the close of the first period, and

this was not sufficient time to remove all the carbon dioxid from the system, as was shown by the high percentage of the gas found in the residual air. It is possible that in this circumstance the air in the hive had a larger percentage of carbon dioxid than that of the sample analyzed. On the 22d the air was passed through the soda lime for nearly three hours prior to the end of the period, in which case the air in the hive had greater opportunity to become like that of the system. Even with a carbon-dioxid content of at least 6 per cent, which was the case on the 21st, the quantity of the gas carried over in the hive to the next period would be much less than 1 liter, which would still leave a wide difference between the figures for carbon-dioxid production in these two days. There is nothing in the data at hand to suggest a reason for this difference. It is interesting to observe that the total of carbon dioxid produced for these two days was almost identical with that of the two days preceding them, when the carbon-dioxid concentration of the air was low.

The proportion of oxygen in the air at the end of each period is also shown in the table. These figures simply show the condition at a given time each day, but they give no definite idea of the proportion of oxygen in the air during the whole day. This would vary hour by hour with the admission of oxygen, the absorption of water vapor and carbon dioxid, and with changes in the temperature of the air, but on the whole would be somewhere in the range between the proportion at the end of one period and that at the corresponding time in the period preceding or following. The figures therefore show that there was a continual increase in the proportion of oxygen from the 13th to the 20th, then a decrease to the 23d.

The low proportion of oxygen in the air at the beginning of the experiment was due to the fact that air rather than oxygen was supplied to the system to replace the carbon dioxid and water vapor removed during the preliminary period and to maintain a sufficient quantity of air in the system while the apparatus was being chilled before the experimental conditions were established. After the experiment began, replacement was made by oxygen until the 20th, when the requisite volume was again maintained by admitting air, in order to reduce the proportion of oxygen in the air of the system. No effect that could be ascribed to changes in the oxygen content of the air was observed until the last day of the experiment. On that day not only water vapor and carbon dioxid, but oxygen also was removed from the system by passing the circulating air through a solution of potassium pyrogallate before returning it to the chamber. This was continued until the proportion of oxygen in the air, which was only 18 per cent at the beginning of the period, was very greatly reduced. After a few hours the circulation of air was stopped and the water vapor and carbon dioxid allowed to ac-

cumulate in the air of the system in which there was a deficiency of oxygen. The effect on the activity of the bees was soon apparent; the temperature curves, which for some reason had begun to rise, very shortly turned in the opposite direction and continued to fall for about 12 hours. The proportion of oxygen was then 12 per cent and it was thought that the bees had probably been suffocated. Eight hours before the time at which the period would regularly end the air of the system was again put in circulation and water vapor and carbon dioxid removed, oxygen being also removed at the same time. This was continued until the close of the period (which was also the end of the experiment) in order that the air of the system might be quite thoroughly freed of carbon dioxid. After the circulation of air was resumed the bees again indicated that they were living, and during the time that the air-purifying system was operating their activity increased until by the end of the experiment the temperature curve had reached as high a point as at any time during the course of the experiment, even though the proportion of oxygen in the air was low. Analysis of the sample taken at the end of the period showed only 7.3 per cent of oxygen.

If the decrease in the activity of the bees in this instance was due to atmospheric conditions in the hive, the cause was probably excess of carbon dioxid and water vapor rather than deficiency of oxygen. Though the proportion of oxygen in the air was decreased from 18 to 12 per cent in 16 hours, it is doubtful if this alone would have an appreciable effect upon the physiological activity of the bees. In experiments with men in atmospheres about as deficient in oxygen as this, there was no noticeable effect upon their metabolism. In these experiments, however, there was no such excess of carbon dioxid and water vapor as in the experiment with the bees.

It is possible, as intimated on page 6, that the reason for the increase in activity of the bees after the circulation of air was resumed may have been physical disturbance. Since it was thought that the bees were dying, movement about the laboratory was somewhat less restricted when the air-circulating device was started, although care was still taken to avoid jarring the calorimeter. The circulation of air through the calorimeter could hardly have caused any disturbance of the bees, because the low rate, while sufficient to keep the air in motion, could not produce any current that would stir the hive. It is also possible that, since the removal of oxygen from the air was continued during this period, the proportion of oxygen in the air eventually became so low that the bees had to respire more rapidly to obtain a sufficient quantity of this gas. It would be expected, however, that this effect would be manifested somewhat later in the period than the time at which activity was renewed.

In considering the circumstances on this last day of the experiment with bees it is interesting to recall observations made in the study of the effect of ventilation on men, that the sensations produced by "bad" air are not experienced when the air is stirred. If this indicates an actual difference in physiological conditions in the different circumstances, then it is not inconceivable that something analogous to this was true of the bees on this day. The stirring of the air when the circulation was resumed may have served to remove some cause of depression that was effective when the circulation was stopped.

SUMMARY.

In the colony of bees under observation in the respiration chamber the expenditure of energy was reduced to the lowest limit by the maintenance of favorable temperature and by the avoidance of all disturbing factors, so far as possible. Under these circumstances, rarely found in the apiary, the energy produced by the bees, as measured by the carbon dioxid and water produced and the oxygen consumed, was greater, according to body weight, than that produced by a man when working at hard manual labor, when we take into consideration the fact that the work was done by only a relatively few of the bees in the cluster. Even assuming that the work of the period were equally divided among the bees, their energy output per unit of body weight is higher than that of the average laborer. When we take into consideration the fact that usually the bees do not have such favorable conditions in winter as these bees had, it is clear that the energy output is enormous in the average apiary.

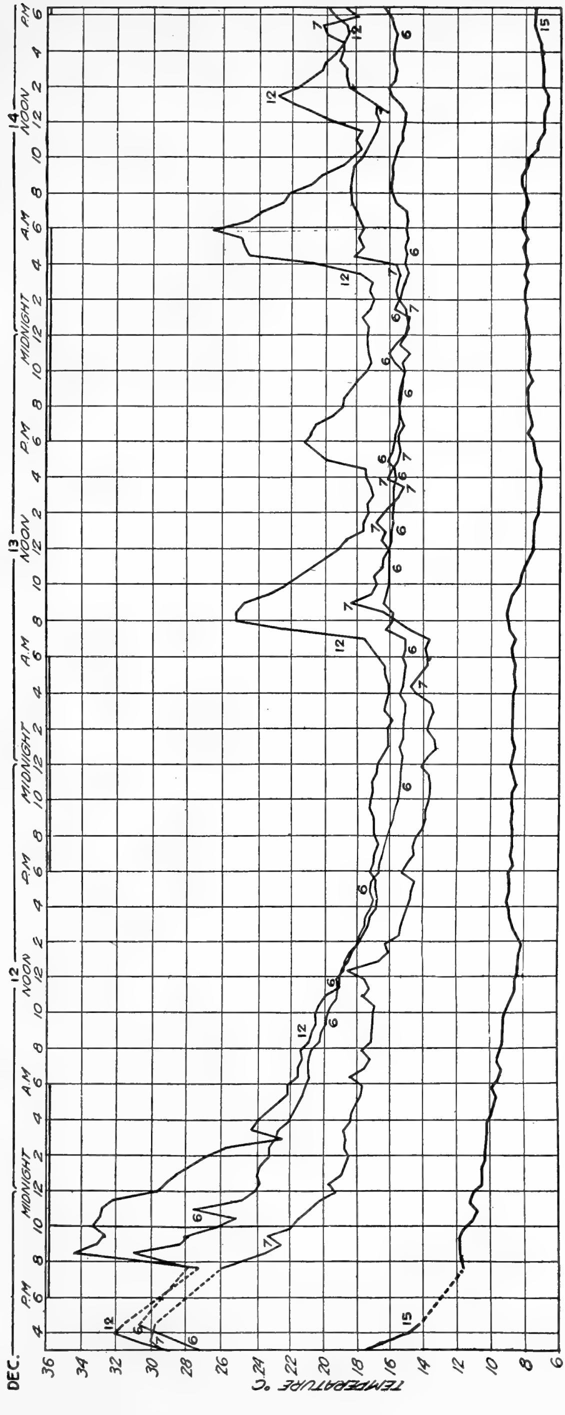

CHART I.—Temperatures shown by thermocouples 6, 7, 12, and 15, from 3 p. m., December 11, to 6.30 p. m., December 14.

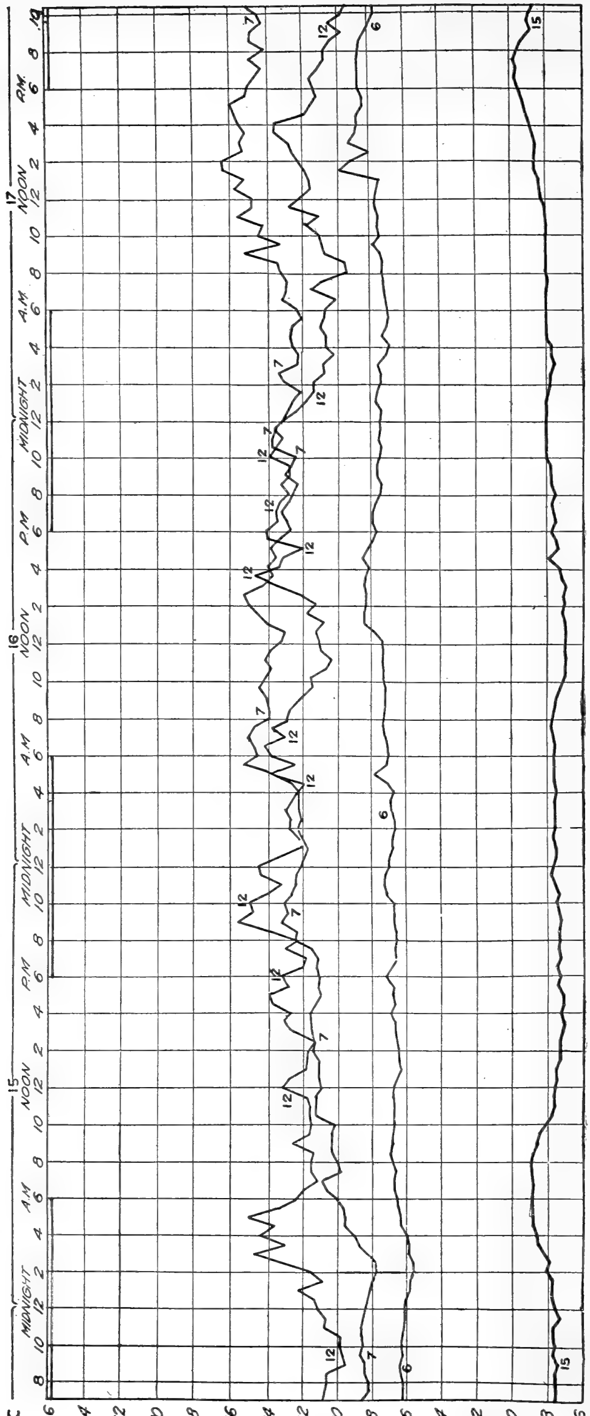

CHART II.—Temperatures shown by thermocouples 6, 7, 12, and 15, from 6.30 p. m., December 14, to 10.30 p. m., December 17.

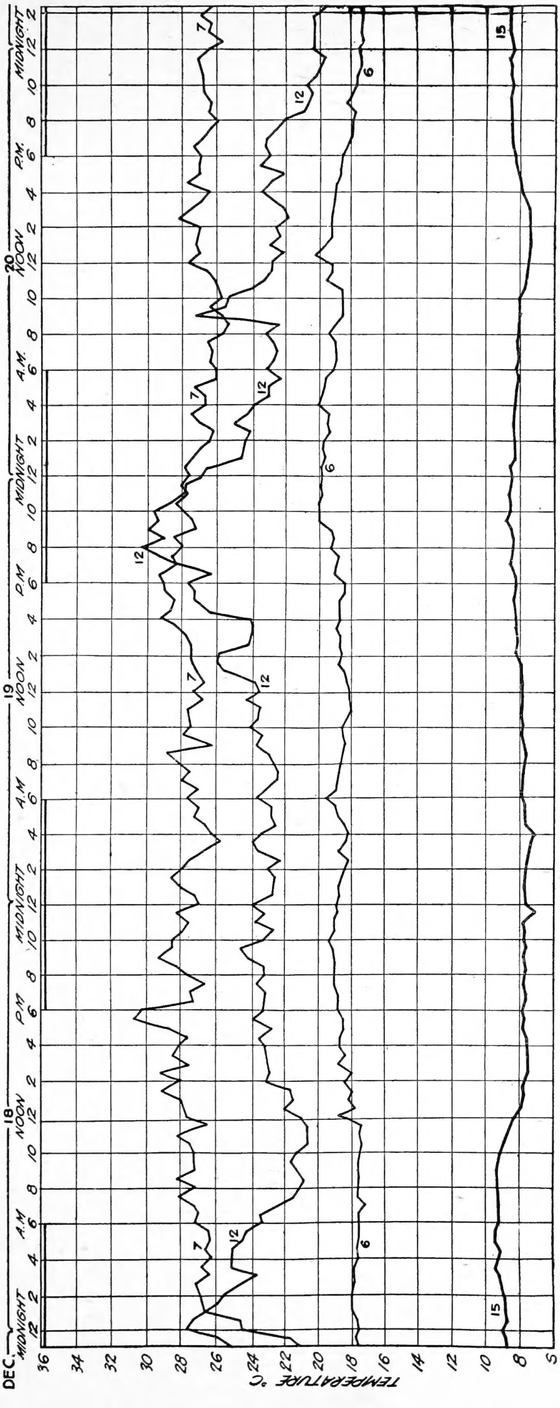

CHART III.—Temperatures shown by thermocouples 6, 7, 12, and 15, from 10.30 p. m., December 17, to 2.30 a. m., December 21.

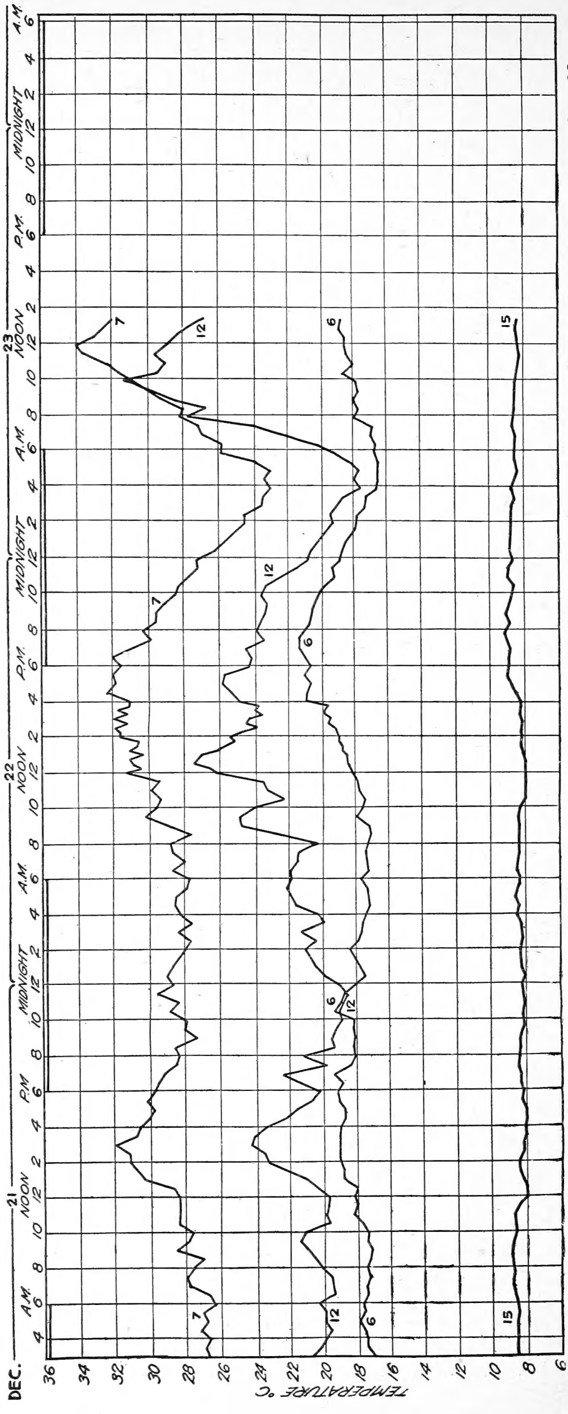

CHART IV.—Temperatures shown by thermocouples 6, 7, 12 and 15, from 2.30 a. m., December 21, to 12.30 p. m., December 23.